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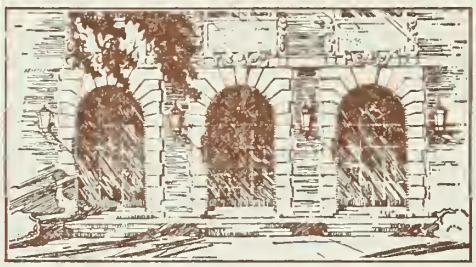

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MARGINAL PRODUCT PRICING IN THE ECOSYSTEM

By

Bruce Hannon

July, 1974

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MARGINAL PRODUCT PRICING IN THE ECOSYSTEM

by

Bruce Hannon

Energy Research Group
Center for Advanced Computation
University of Illinois at Urbana-Champaign
Urbana, Illinois 61801

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ABSTRACT

Through an analogy with economics, a comparitive static theory is developed for ecological systems. The basic assumption is that components of the ecosystem behave in such a way as to maximize their storage with respect to their material flows. This concept leads to the theory that biological component will adjust its marginal productivity with respect to each of its energy flows to be equal to the energy intensity (price) of that flow. The result is additional information about the relationships between energy and mass flows in the ecosystem.

Equilibrium and cropping conditions are included and a connection with input-output theory is made. Example systems are developed to illustrate the theory.

1. Introduction

A. General

Man is part of the ecosystem. His dislikes and desires, his strategies and opportunitites, his competition and cooperation, are as natural as such behavior is for any other living component. It should not be futile therefore to attempt to discover analogies between the view man holds of his system and the view of any other living component. The danger of any such analogy lies with the point of view of the writer: he is necessarily peering from within the system of man and gazing upon the system of living things. The degree to which these positions are aligned is reflected in the accuracy of the analogy.

Basically man views the operation of his system through economics. He establishes value between buyers and sellers by the amount of the system currency needed to produce a given quantity of physical transaction. The ratio of the amount of currency to the amount of transaction is called the price. By carefully manipulating the quantities and prices of its inputs with respect to the quantities and prices of its outputs, an economic production unit may achieve a net surplus of income called profit, after maintenance costs are paid. The apparent goal of such a unit is to maximize its profit with respect to the magnitudes of its product flows, subject to constraints of supply-demand balance and its production capabilities. The profit is used to expand the size of the unit. But as groups of these units grow, they eventually experience diminishing output per unit of input and the zero profit condition is finally reached. This is called the equilibrium point for the group and it

possesses various degrees of stability. The background of economic theory has been well developed and well summarized. Examples are: Bailey (1962); Henderson and Quandt (1971); Samuelson (1965); Stigler (1961).

In a somewhat similar manner a biological component may be viewed as an economic production unit. If we let energy be the currency or measure of value, then "price" is the amount of energy contained in a unit of production. Successful, growing components realize profit when they are able to store energy; thus I assume that energy storage in the biological component is analogous to profit in the economic unit. The principal assumption of this paper is that biological components maximize energy storage with respect to their material flows. This concept makes biological components one of Dyson's (1971) energy "hangups," those cases where energy is slowed in its seemingly inexorable flow toward a uniform universal temperature.

Differences between economic and the ecological systems are evident. Because of the assumption that energy is biological currency, input energy in the biological system is roughly the same as "costs" or dollar value of the inputs in the economic system. Output energy must be thought of as a cost in the biological system, while the dollar value of output represents an income in economics. The differences arises from the fact that currency and commodities flow the same direction in the biological system but opposite in the economic system.

The advantages of the analogy are real. An ecologist models the relationships between the energy flows to and from a biological component. With the assumption of storage maximization he can determine at which of the many possible flow conditions the component will be operating: that is, a component chooses to adjust the rate at which its production function

varies with each of its material flows such that this rate would be equal to the energy content of a unit (price) of the particular flow. This is the condition for maximization of energy storage in the component. The removal of storage (cropping) should not change this phenomena as long as the cropping does not damage the storage mechanism. Hopefully, one can collectively simulate each individual, species, or trophic levels with such a mathematical concept, but the additional assurance that system production is equal to system consumption is needed.

B. Definitions

By the term biological component I mean that individual, species or trophic level capable of sustaining its own life by interaction with the remainder of the ecosystem (a collection of biological components, energy sources and sinks). Such a component is displayed in Figure 1, with its inputs, $\tilde{e}_j$ and its outputs $\tilde{p}_j$, the production flows and $\tilde{r}_j$, the respiration flows. Energy flow is defined as the amount of energy transported in the specified period of time. The energy input $\tilde{e}_j$ is the sum of the masses of the individual flows from the ith components to the jth component, x_{ij}, times their respective energy content or price, ε_{ij}. The output $\tilde{p}_j$ is the sum of the production mass flows from the jth component to the kth component, x_{jk}, times their respective energy content or price, ε_{jk}. The remaining output is the respiration flow $\tilde{r}_j$ which is the sum of the energy used for feeding $\tilde{r}_j^f$, the stored energy, $\tilde{r}_j^s$, the exported energy, $\tilde{r}_j^e$ (non heat energy which leaves the system)

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*The ~ over the letter indicates a vector element (alternative is to italicize).

and the subsistence or maintenance energy $\tilde{r}_j^b$, which must be expended regardless of the other flows. The feeding energy is the sum of the input quantities x_{ij}, times the respective energy expended in the quest for a unit of x_{ij} by the jth component, ℓ_{ij}. It is also possible for the component to expend energy to avoid or limit predation. This case can be described in exactly the same manner as is done by the ℓ_{ij}. I omit the possibility from this discussion to preserve the simplicity of the presentation. $\tilde{r}_j^s$ is the equivalent of profit in the economic system, and $\tilde{r}_j^e$ is equivalent to the payment to stockholders or governments.

2. Theory

A. General

The first assumption is that time can be explicitly excluded from the process. Thus I assume that the processes described below obtain during some clearly specified period of time. Time is introduced implicitly through the variation of the basic system inputs such as that of the sun.

In writing the equation for energy balance across the jth component, we always have energy input equals energy output or

$$\tilde{e}_j - \tilde{p}_j - \tilde{r}_j = 0 \qquad (1)$$

or from Figure 1,

$$\sum_i^n \varepsilon_{ij} x_{ij} - \sum_k^m \varepsilon_{jk} x_{jk} - \sum_i^n \ell_{ij} x_{ij} - \tilde{r}_j^s - \tilde{r}_j^b - \tilde{r}_j^e = 0 \qquad (2)$$

where there are n total inputs and m total outputs and $\varepsilon_{ij} x_{ij} = p_{ij}$, the specific production energy flows.

The second assumption is that $\tilde{r}_j^b$ is a constant with regard to each of the production flows over the time period involved. $\tilde{r}_j^b$ is effectively a function of the size of the jth component and therefore the second assumption requires that the component size not change appreciably. Equations (1) and (2) could be rewritten to include a size parameter, but such an introduction would not affect the general conclusion of this paper.

The third assumption is that the functional relationships between the amount of input x_{ij} and the output flows x_{jk}, are known accurately for the selected time period. Such a relationship requirement, called a production function, is not unusual. Ultimately, in mathematical modeling, one must assume that the behavior of the component at some level is known only from experimental analysis. The final difficulty lies in the experimental determination of the functional relationship since many experiments are performed under the assumption of constant conditions. Any functional relation between input and production would necessarily vary with the ambient temperature, the food availability and conditions, (i.e., the extent to which the amount of a species consumed affects its ability to produce), the seasons, the age and physical condition of the component, etc. Examples of such relationships have been developed by Anway (1974). Other biologists have begun to use indifference curves as a means to determine relationships between the input functions (Covich, 1972). In the "examples" section of this paper, I have used simple quadratic relations to facilitate a demonstration of the theory but not the probable complexity of the production function.

The fourth assumption is that it is the nature of a biological component to maximize stored energy with respect to its material flows. This assumption simply seems reasonable from general observation. It is based on an apparent natural acquisitiveness which living components seem to have. Increased energy storage would seem to provide increased component stability during periods of fluctuating inputs or excessive production. Watt (1973) reasoned along with Margalef (1968) that increasing size meant increasing energy use efficiency, a principle which tends to support the fourth assumption.

For a given available energy input, increased component size eventually means fewer components despite the increasing efficiency. Fewer components means a lower diversity which can produce a more general form of instability. Thus it seems likely that a component will eventually cease to grow in an effort to trade individual stability for that of the group, a possible demonstration of Ardrey's (1966) "biological morality." The process of storage maximization with respect to production is assumed to hold for each component while the system as a whole approaches a zero storage rate condition.

By combining ε_{ij} and ℓ_{ij} into a net energy price* (see Figure 2) $\varepsilon'_{ij} = \varepsilon_{ij} - \ell_{ij}$, and by combining $\tilde{r}^{e}_{j}$ with $\tilde{r}^{s}_{j}$, equation (2) can be restated

$$\sum_{i}^{n} \varepsilon'_{ij} x_{ij} - \sum_{k}^{m} \varepsilon_{jk} x_{jk} - \tilde{r}^{b}_{j} = \tilde{r}^{s}_{j} \quad . \tag{3}$$

Equation (3) reflects the principle of conservation of energy. It states that the energy difference between all inputs and all outputs less the fixed maintenance energy requirement is equal to the energy removed from flow (storage and export from storage) by the jth component.

To simplify the presentation of the maximization procedure let all inputs and outputs for the jth component be denoted x_p and all input and output energy prices be ε_p. Inputs contribute a positive sign and outputs a negative sign. Also note that ε_p for an input is a net energy price. Thus equation (3) can be rewritten for the jth component as

$$r^{s} = \sum_{p=1}^{m+n} \varepsilon_p x_p - r^{b}, \tag{4}$$

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*conceivably negative (e.g. when water is an input)

where n is the number of inputs and m is the number of outputs.

Let a typical production function F^i for the jth component be given as

$$F^i = F^i(x_p) = 0, \tag{5}$$

where i varies from 1 to q and q is the number of separately given production functions. The $\tilde{r}^s$ and F^i are assumed to have continuous first partial derivatives and the Jacobian of the F^i must have rank q (Aoki, 1971, p. 171). Thus we can employ the Lagrange technique for maximization. We form the function

$$V = \tilde{r}^s + \sum_{i=1}^{q} \lambda_i F^i \quad , \tag{6}$$

where the λ_i are the Lagrangian multipliers.

The partials of V with respect to each x_p must be zero at the extrema. Thus

$$\frac{\partial V}{\partial x_p} = \varepsilon_p + \sum_{i=1}^{q} \lambda_i \frac{\partial F^i}{\partial x_p} = 0 \quad . \tag{7}$$

These m + n equations are the basic requirements for storage extrema. I call the term, $-\sum_{i=1}^{q} \lambda_i \frac{\partial F^i}{\partial x_p}$, the marginal productivity of component j with respect to flow x_p. It is equal to the energy price ε_p, which may be a function of the x_p. To select the maximum level from the extrema given by equation (7) further restrictions are needed. All eigenvalues of the Hessian matrix of V must be negative for $\tilde{r}^s$ to be a maximum (Aoki, 1971, p. 21). This condition plus those which assure the existence of the λ_i constitute the necessary and sufficient conditions for

the existence of a maximum for the storage function. Evaluating the general Hessian matrix for a given component is a tedious process. Nevertheless, such a process may prove fruitful as it will provide certain critical relationships among the elements of the production function.

A final equation, stemming from the principle of mass conservation is derived from equation (3), where ε_j is the average energy content of a unit of component j.

$$\sum_i^n x_{ij} - \sum_k^m x_{jk} - \frac{(\tilde{r}^b_j + \tilde{r}^s_j)}{\varepsilon_j} = 0 \quad . \tag{8}$$

Equation (8) allows calculation of the physical amount of material stored, once the x_{jk}, ε_j and $\tilde{r}^b_j$ are known.

B. Competition and Monopoly

The economic requirements for perfect competition - homogeneous products, numerous components, each with perfect information and zero cost movement to and from the system - probably prevail more exactly in natural system than in economic systems, at least at the level of the individual members of a species.

The chief characteristic of a highly competitive component would be the adjustment of flow and not price, to meet the requirements of equation (7). An individual member of a species cannot vary (except possibly over very long periods of time) the energy prices (intensities) of its inputs and outputs. Thus, to be a storage maximizer, these individuals must vary the relative levels of their product flows.

A group of species, however, viewed as a single component (trophic level) is not competitive. Accordingly it must vary both its

energy prices and its relative output levels to reach the storage maximizing conditions. The price-output relations are, however, uniquely determined through equations (4) and (5). This behavior is termed "monopolistic" in economics.

The nature of the interdependence between the outputs of various individuals, species or trophic levels is of concern in determining the scope with which the appropriate production function must be resolved. I believe that since the components of these groups compete generally for the same resources that the value of the ℓ_{ij} in the net energy price of each input for each component reflects the relative difficulties of obtaining the desired input. Since the desired inputs are related to the component outputs through individual production functions, all outputs of the competing components should be suitably related to each other through their inputs and net input prices. Accordingly there should be no need to include every product flow in a trophic level, in the production function of each species. This results in a considerable simplification of the experimental techniques which must be employed to determine the production functions.

C. Supply, Demand and Equilibrium

Define a trophic level as a collection of species which feed from the same set of sources and which do not produce for each other. This is a slightly different definition from Odum (1971) who defines a trophic level by function and thus a given species may be in two trophic levels at once. The definitional difference can be reconciled by defining such a species as two subspecies, each in a separate trophic level.

The juncture of trophic levels thus defined is similar to the "market" in economics. The trophic level is comparable to an industry. Each industry is made up of a certain number of firms comparable to species. The production functions (F^i) relating the x_{ij} and x_{jk} for each species may be nearly identical but their "market" price may vary because of variation of their ℓ_{ij}. The average output price of the trophic level may vary because the price of the species varies and/or because the proportions of the trophic level output varies with the species.

The system constraint is that supply must equal demand between all trophic levels while each species (and each individual) sets its marginal productivity with respect to each flow equal to the price of that flow.

These are the conditions of short term equilibrium. Long term equilibrium requires one additional constraint: energy storage in the system is zero. A further long term requirement is that $\tilde{r}_j^b$ be considered a variable part of the respiration. I assume that it can be identified with the ℓ_{ij}.

Exploiting this concept will yield the production and respiration flows and the energy prices for each species and each trophic level as the system progresses toward equilibrium (zero storage) and each component maximizes storage with respect to its product flows as it evolves.

D. Cropping

Exporting biomass from the biological system is one of man's principle activities. He generally exports from storage (e.g., sustained yield cutting of forests, agriculture, etc.). Exporting is usually done at the rate (time) at which the cropped component produces most rapidly.

The components are often specialized by selective breeding or the system modification (e.g. selective clear cutting in forests), to increase this rate.

In the context of this paper, cropping from storage has been thought of as removing from the system a constant fraction of that energy which is being diverted into storage. In so doing the component is fixed on its evolutionary path toward equilibrium. The component continuously tries to reach the size for which additional storage is not needed. This process is dexcribed by modifying equation (3) thus,

$$(1 - c_j)[\sum_i^n \varepsilon'_{ij} x_{ij} - \sum_k^m \varepsilon_{jk} x_{jk} - \tilde{r}_j^b] = \tilde{r}_j^s \ ,$$

where c_j is the fraction of storage being cropped. It is probable that cropping could be severe enough to cause instability in the producer.

Equation (7) follows identically since $c_j < 1$. Therefore, cropping from storage does not disturb the component's operation levels for maximizing storage, whether the component is acting as a monopolist or a perfect competitor.

E. Feeding Strategies

A component may be faced with a choice of prey for a particular one of its needed input groups. Each choice has the same energy price, ε, but each requires a unique feeding effort, ℓ, per unit of prey. Such a case could arise for example if the desired input were located at various sites at increasing distances from the base territory of the predator, or if the input were housed in shells of various thicknesses, etc. Presuming that the component has perfect information (and is able to process this information) about its prey, and further assuming that the

component wishes to minimize the energy expended per unit of energy captured, we can predict its feeding behavior.

First, however, it is necessary to form what appear to be rational assumptions about the manner in which ε and ℓ vary with the amount consumed, x. It seems reasonable to assume that ε will decrease slowly and ℓ increase rather exponentially as the preying progresses. The result $\varepsilon' = \varepsilon - \ell$ is therefore a declining function of x. These phenomena are shown in Figure 2.

Next I classify the net energy price functions of the various choices on the same chart as shown in Figure 3. In Figure 3, I assume as an example that there are three possible choices whose net energy prices are ε_1', ε_2' and ε_3'. Note that the area under the ε' vs x curve is the "net" energy input to the component. Under an assumption that the component strives to maximize the net energy input, it will follow a path of largest possible ε'. This means that as the component feeds down the ε_1' curve it will switch from the ε_1' curve to the ε_2' curve at the point b since the slope of the ε_2' curve at point a is greater (algebraically) than the slope at point b on the ε_1' curve. The same situation does not exist at points c and d on the ε_3' and ε_2' curves so the component continues to feed along ε_2'. The slopes of these curves become equal at points e and f, however and the component begins feeding along the ε_3' curve at point g. Thus the upper curve in Figure 3 becomes the feeding path for maximizing net energy input. It provides the most likely functional relationship between ε' and the corresponding input. Such knowledge is useful in conjunction with the maximum energy storage principle in the determination of output energy prices as will be shown in the examples.

F. Relationship with Input-Output Theory

Hannon (1973) developed an expression for the direct and indirect energy flows relating the respiration energy flow, $\tilde{r}_k$ with the total input flow $\tilde{e}_j$,

$$\tilde{e}_j = \sum_k^m (I-G)^{-1}_{jk} \tilde{r}_k = \sum_k^m p_{jk} + \tilde{r}_j \quad , \tag{9}$$

where G is a production matrix whose elements p_{jk} are assumed to be

$$p_{jk} = g_{jk} e_k \quad . \tag{10}$$

Substituting equation (10) into equation (9) gives

$$\tilde{e}_j = \sum_k^m g_{jk} \tilde{e}_k + \tilde{r}_j \quad . \tag{11}$$

Comparing this result with equation (2) we see that

$$g_{jk} \tilde{e}_k = \varepsilon_{jk} x_{jk} \quad . \tag{12}$$

If I write $\tilde{e}_k = \varepsilon_k x_k$, where ε_k is the average energy price of the tot mass flow, x_k, into component k, equation (12) becomes

$$g_{jk} = \frac{\varepsilon_{jk} x_{jk}}{\varepsilon_k x_k} = \frac{\varepsilon_{jk}}{\varepsilon_k} \; g'_{jk} \quad , \tag{13}$$

where $x_{jk} = g'_{jk} x_k$ is the mass equivalent of equation (10).

Thus if the energy prices of the inputs and outputs and the g'_{jk} can be determined from equations (5) and (7), the g_{ik} of the energy production matrix are known. Then the component energy interdependence (direct and indirect) can be demonstrated for the given time period.

3. Examples

A. Maximum Component Storage

Assume that a component has one input, x, and two outputs, x_1 and x_2 and that they are related by

$$x^2 = ax_1^2 + bx_1 + c \quad \text{and}$$

$$x_1 = gx_2 \ ,$$

where a, b, c and g are given constants.

Rewriting the production function in a more suitable form

$$F^1 = x^2 - ax_1^2 - bx_1 - c = 0 \ ,$$

$$F^2 = x^2 - ag^2x_2^2 - bgx_2 - c = 0.$$

Applying equation (7) and assigning negative values to input terms yields

$$\varepsilon' + 2x(\lambda_1 + \lambda_2) = 0 \ ,$$

$$+ \varepsilon_1 + \lambda_1(-2ax_1 + b) = 0 \ ,$$

$$+ \varepsilon_2 + \lambda_2(-2ag^2x_2 + bg) = 0 \ ,$$

where ε', ε_1, and ε_2 are the energy prices of the input (net price) and the outputs respectively. These equations yield a special relation between the flows and the energy prices,

$$\varepsilon' = \frac{2(\varepsilon_1 + \varepsilon_{2/g})x}{b - 2ax_1} \ .$$

The Hessian matrix of V,

$$\begin{bmatrix} 2(\lambda_1 + \lambda_2) & 0 & 0 \\ 0 & -2a\lambda_1 & 0 \\ 0 & 0 & -2ag^2\lambda_2 \end{bmatrix}$$

must be negative to insure that a maximum of $\tilde{r}^s$ exists. Therefore we have the following conditions

$$\frac{-\varepsilon'}{x} < 0; \quad \frac{a\varepsilon_1\varepsilon'}{x(\varepsilon_1 + \varepsilon_{2/g})} < 0; \quad \frac{ag\varepsilon_2\varepsilon'}{x(\varepsilon_1 + \varepsilon_{2/g})} < 0.$$

The first condition is automatically met since ε' and x must be positive. If g is assumed to be positive, a must be negative to satisfy the last two conditions.

B. Multiple Components

Assume that we wish to resolve the energy prices when the input flow is given for the simple system shown in Figure 4. The supply-demand requirement is satisfied by the construction of this figure. Assume further that each component input x_{ij} can be described as

$$x_{ij}^2 = a_{ijk}x_{jk}^2 + b_{ijk}x_{jk} + c_{ijk}$$

where the a, b, c and g are given constants and cropping is zero. Here x_{jk} is the main output flow. Other output flows are directly proportional to x_{jk}, e.g., $x_{jk} = g_{j\ell}x_{j\ell}$.

Applying equation (7) we find for each component:

Component One (one input and two outputs)

The example in Section 3-A applies and therefore

$$\varepsilon'_{s1} = \frac{2\left(\varepsilon_{12} + \varepsilon_{13}/g_{13}\right)x_{s1}}{b_{s12} - 2a_{s12}x_{12}}$$

$$x_{12} = g_{13}x_{13}.$$

Component Two (one input and one output)

From Section 3-A with $g = \infty$, we have,

$$\varepsilon'_{12} = \frac{2\varepsilon_{23}x_{12}}{b_{123} - 2a_{123}x_{23}}.$$

Component Three (three inputs and one output)

Applying equation (7) gives,

$$\varepsilon_{33} = \frac{\varepsilon'_{13}}{2x_{13}} (b_{133} - 2a_{133}x_{33}) + \frac{\varepsilon'_{23}}{2x_{23}} (b_{233} - 2a_{233}x_{33})$$

$$+ \frac{\varepsilon'_{33}}{2x_{33}} (b_{333} - 2a_{333}x_{33})$$

Thus if the input energy price (net) and flow from the sun is known and the output energy are given, the four ℓ_{ij} can be determined from the above four equations.

The possibility of equilibrium can then be tested. If the system is in equilibrium, then

$$\tilde{r}^{s}_{1} + \tilde{r}^{s}_{2} + \tilde{r}^{s}_{3} = 0$$

and $$\varepsilon_{s1}x_{s1} = \ell_{12}x_{12} + \ell_{13}x_{13} + \ell_{23}x_{23} + \ell_{33}x_{33}.$$

Note that ε_{s1} can be determined from the known energy received from the sun divided by the mass flow into component one caused by the sun.

Second order conditions as demonstrated in section 3-A add constraints to the elements of the production functions.

C. Linear Production Functions

Statistical analyses of flows thru components are probably the most obvious means of obtaining simple production functions. Linear multiple regression analysis can be used to produce linear or product forms of production functions. The product models reduce to linear form with logarithms.

It can be shown that the Hessian matrix of the Lagrangian functions with linear constraint (production) functions will be zero. Thus a maximum storage configuration, if one exists, can be found only through the technique of linear programming. That is, if the production functions are

$$\tilde{x} = A\tilde{y} + \tilde{b}$$

where vectors x, y are the dependent and the independent inputs or outputs respectively, $\tilde{b}$ is a vector of constants and A is the matrix of correlation coefficients, the linear programming problem is then to maximize the storage function $\sum_{p=1}^{q} \varepsilon_p \tilde{z}_p$ subject to the constraint of the production functions. Here $\tilde{z}$ takes the values of $\tilde{x}$ and $\tilde{y}$ and q is the total number of inputs and outputs.

Conclusions

If, in modeling ecosystems, we can admit the assumptions that the functional relationships between input and production are known, that each biological component acts in such a way as to maximize energy storage with respect to its product flows over a specific period of time, that supply equals demand for all production, and the production functions are known, then we have enough information to determine all the product flows and energy prices in the system. Additional constraints are placed on the production function by the second order maximization conditions and if it is known that the system has evolved to the zero storage condition. The mass balance equations add further information about the system.

Energy price, as defined by the energy content of a unit of the particular component's product flow, is constant in competitive systems and varied in monopolistic systems. When a component is operating as a storage maximizer, it sets the marginal productivity with respect to each product flow equal to the energy price of that product.

Cropping the storage of any component can be easily handled in the above theory. It is assumed that cropping can continue indefinitely if the storage is not depleted below a critical level.

When a component is faced with a variety of choices of modes to obtain the same type of input, it is speculated that it will follow the path of maximum net energy input. The construction of such a net energy curve provides the functional relationship between each input and its energy price.

The connection of the theory of this paper to linear-input output theory is demonstrated. The energy production coefficients can be determined

from the mass flows, the production function and the maximum energy storage principle.

A set of hypothetical components have been described in several examples to demonstrate the application of the energy storage maximizing principle and its use in resolving the likely energy and mass flows in an ecosystem. The condition of system equilibrium was demonstrated for a three component system.

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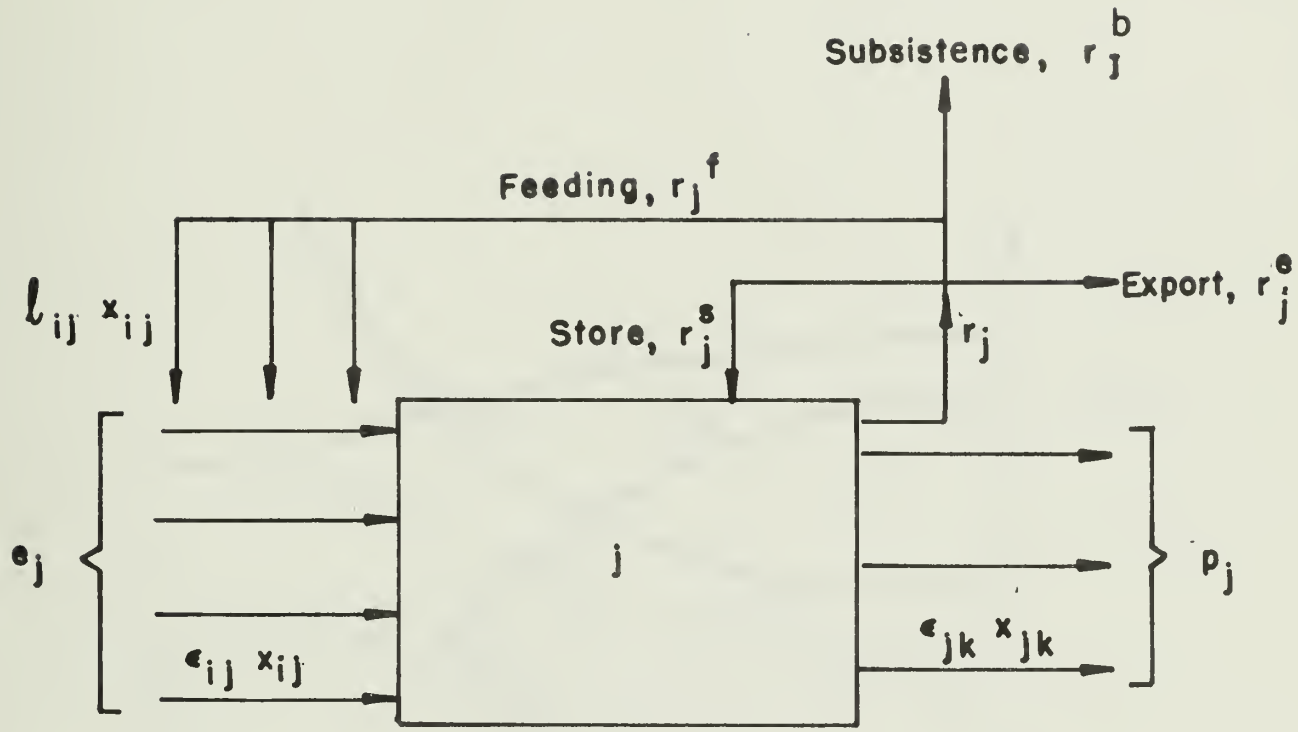

Figure I. Energy Flows in the jth Biological Component

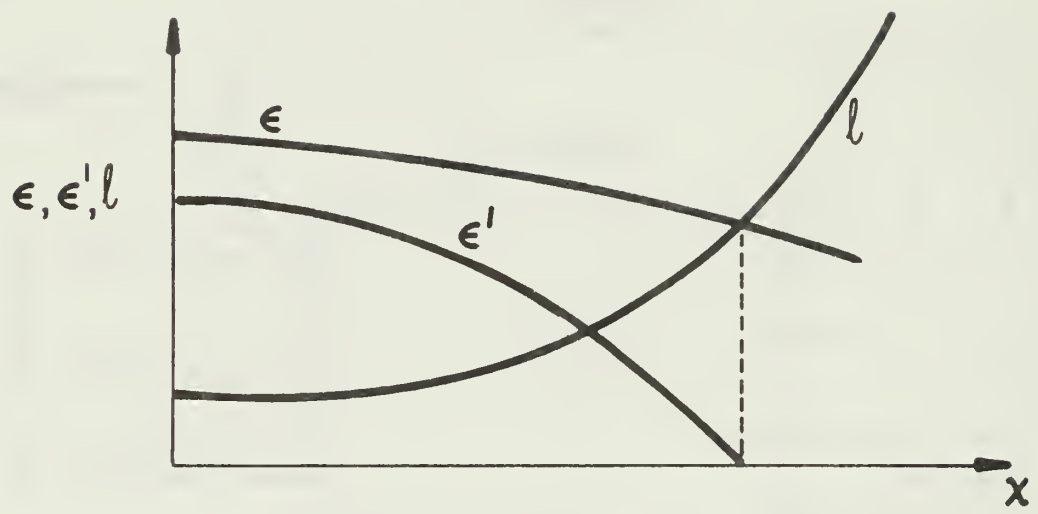

Figure 2. Energy Price, ϵ, Feeding Effort, ℓ, Net Energy Price, ϵ'.

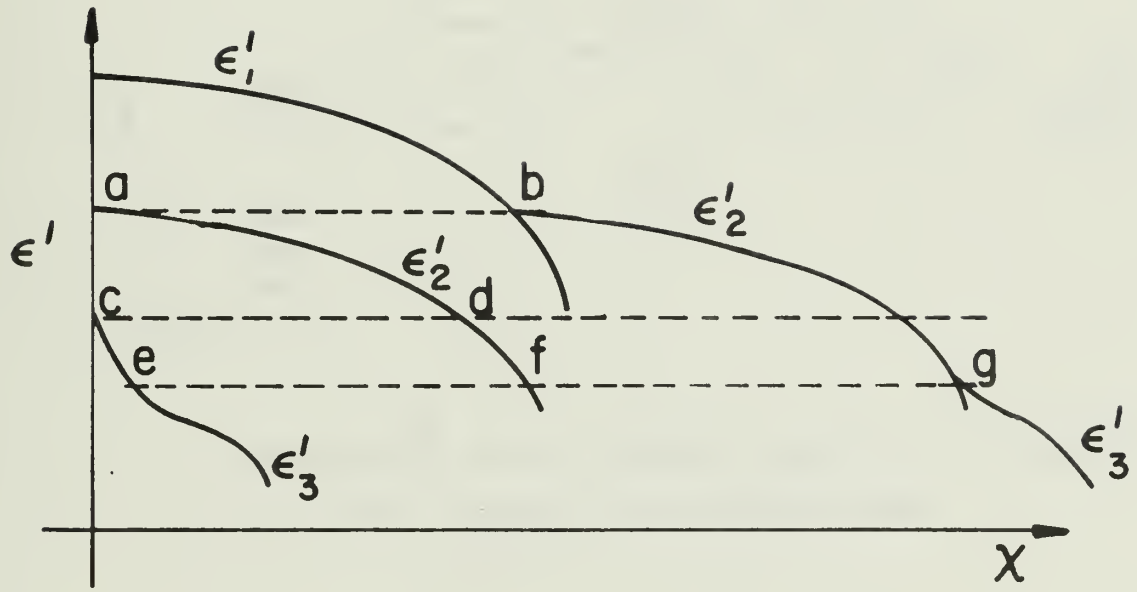

Figure 3. The Optimum Energy Feeding Strategy

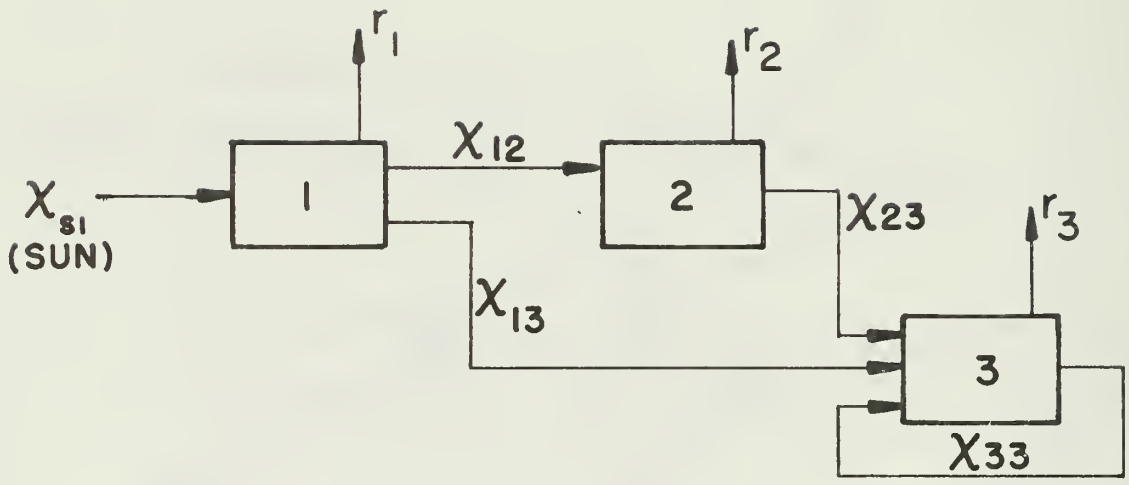

Figure 4. A Simple Model of an Ecosystem With Balanced Energy Flow.

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